

PARENTAL INVESTMENT IN SWAN GEESE IN AN URBAN ENVIRONMENT

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ABSTRACT.—I studied brood-rearing behavior of introduced Swan Geese (*Anser cygnoides*) in Heidelberg, Germany during 2002 and 2003. Two hypotheses were tested: (1) division of labor between males and females is similar to that of wild *Anser* species, and (2) parental investment (vigilance behavior) is adjusted for brood size. I used 10-min sessions of focal animal sampling during which I simultaneously recorded the behavior of the male, the female, and a majority of the juveniles every 15 sec. Division of labor was similar to that observed in wild *Anser* populations: males were more vigilant whereas females spent more time feeding during the first 4 weeks of brood-rearing. As brood-rearing progressed, vigilance and agonistic behavior by both males and females decreased, whereas juveniles decreased feeding and increased vigilance. Adults (males and females combined) adjusted vigilance for brood size. A general linear model showed a significant influence of both brood size and brood age on parental vigilance. Received 12 February 2004. Accepted 12 July 2006.

During brood rearing, females of most species of wild *Anser* geese usually spend more time feeding than males to compensate for energy loss during incubation. Males spend more time being vigilant, i.e., looking for predators (Afton and Paulus 1992). This division of labor by gender was found in time budget studies of many goose species (Afton and Paulus 1992).

Concerning brood size, larger groups of goslings should receive more vigilance by their parents than smaller groups as parental investment is considered to be “shared” (Lesells 1987). This hypothesis suggests that parental care might be adjusted for brood size by devoting more time to vigilance as brood size increases (“shared” parental investment). The “unshared” parental investment hypothesis suggests that parental vigilance should not be adjusted for brood size, since any time devoted to vigilance benefits all goslings simultaneously, regardless of brood size. Some empirical tests found an adjustment of parental investment (e.g., the level of vigilance) to brood size (Sedinger and Raveling 1990, Forslund 1993, Siriwardena and Black 1999) and others did not (Lazarus and Inglis 1978, Lesells 1987, Schmutz and Laing 2002). However, gosling age is another important variable since mortality of goslings is highest during the first 2–3 weeks of life (Owen 1980, Forslund 1993).

Behavior of introduced geese has rarely been studied (e.g., Randler 2003a, 2003b), and little is known about their brooding behavior. Studies of introduced geese in an urban environment, where most natural predators are absent, may clarify the complimentary hypotheses of parental care in geese. Furthermore, parental investment in neither wild nor introduced Swan Geese (*Anser cygnoides*) has been examined. Since this species is critically endangered (Goroshko 2001), studies of introduced populations may be of conservation interest. The objectives of this study were to examine (1) whether parental care (time budgets and division of labor between males and females) of introduced Swan Geese is similar to that of wild populations, and (2) the relationship between brood size (number of goslings) and parental care (as measured by vigilance).

METHODS

The Swan Goose is a non-native species in Europe, having been introduced in the 18th century (Delacour 1954). The study flock in Heidelberg, southwestern Germany (8° 41' E, 49° 25' N) was established in the 1990s. The birds breed on an island in the Neckar River and soon after hatching, families move to feed on a lawn which extends 1.1 km along the river. In 2002 and 2003, I studied 13 families of Swan Geese (140 individuals in 2002 and 174 in 2003) during brood rearing (Randler 2003a, 2003b).

I used instantaneous focal animal sampling (Altmann 1974) to detect differences between males and females, and identify rare behaviors

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that may be overlooked during flock scans (Baldassarre et al. 1988). Sampling sessions were 10-min/family, during which I recorded the behavior of the male, female, and a majority of the juveniles. Goslings could not be identified individually and I recorded the behavior displayed by the majority of the brood at each instantaneous sample (Schmutz and Laing 2002). The order of sampling families was random. I used 15-sec sampling intervals because this interval provides data that are close to continuous observations (Pöysä 1991). I recorded the following behavioral categories (adapted from McWilliams and Raveling 1998): feeding, resting, walking, comfort behavior (preen, stretch, shake, or scratch), vigilance (neck stretched upward to full length), and agonistic interaction (intra-specific aggressive encounters). Sampling was conducted between 0900 and 1600 hrs (Central European Summer Time) and only when families were on land. If disturbed during sampling (e.g., by dogs; Randler 2003a), families escaped into the water and sampling continued (if necessary) after the geese returned to land. Some bias may be present because data collection was only done during certain daytime periods. This seems unlikely, because time of day does not strongly influence behavior of families with goslings (Lazarus and Inglis 1978, Forslund 1993, Schmutz and Laing 2002).

I separated samplings into 4-week periods of brood rearing (weeks 1–4, 5–8, and 9–12), because parental investment may differ between these periods (Forslund 1993) and goslings were more prone to predation during their first weeks of life (Owen 1980). I chose these sampling periods because at 8 weeks, most juveniles were close to fledging (i.e., capable of sustained flight; Kolbe 1999). Family bonds extend over the brood rearing period and sampling during week 9–12 allows comparison of the brood rearing period with the post-fledging period.

Some studies report between-year differences in time budgets (Schmutz and Laing 2002). Because vigilance did not differ between years I pooled years. An unknown number of individuals may have been sampled in both years and my data may include replicated observations of the same birds. In addition to the 6 (2002) and 7 (2003) families

studied, I also sampled 17 non-breeders of unknown gender between 31 May and 26 June 2002 using the same focal-animal sampling method.

Gender of adults was assigned by knob size, bill size, body size, and behavior. Females had shorter and thinner bills, and shorter necks (Madge and Burn 1988, Ogilvie and Young 1998); males swam behind broods (Bauer and Glutz von Blotzheim 1968, Rutschke 1997). Family sample sizes by periods were 13 (weeks 1–4), 8 (weeks 5–8), and 9 (weeks 9–12); I sampled each family between one and five times during each period. I first calculated the mean for each family (male, female, juveniles) by sampling period and then calculated the means of the three sampling periods. Parental vigilance is the mean of male and female vigilance. Some post-hatching brood amalgamation took place, at times forming families including 3 adults. One “family” of 13 juveniles was led by 4 adults. I did not use amalgamated families in the analyses.

I expressed behaviors (e.g., feeding, vigilance, etc.) as percentages of total time budget (square-root arcsine transformed). To compare percentages between different groups, I used the Mann-Whitney *U* test on untransformed data and, to compare dependent variables, I used Wilcoxon matched-pairs signed rank test. I used Pearson’s correlation to examine the relationship between vigilance and brood size (\log_{10} transformed). I used a general linear model (GLM) with year and period as fixed factors, number of juveniles (\log_{10}) as a covariate and parental care (vigilance) as the dependent variable. I used R^2 as a measure of explained variance. I used SPSS version 11.0 to analyze the data (Bühl and Zöfel 2002) and set statistical significance at $P < 0.05$.

RESULTS

The first goslings appeared on the feeding grounds during the last 10 days of May. Brood sizes did not remain stable during the study period because of predation. I observed two unsuccessful predation attempts, one by Carrion Crows (*Corvus c. corone*) and one by Yellow-legged Mediterranean Gulls (*Larus michahellis*), both of which bred nearby. Brood sizes were 4.3 ± 1.4 ($\bar{x} \pm \text{SE}$) in 2002 and 3.5 ± 0.7 in 2003 during week 1–4.

TABLE 1. Time budgets (%; means \pm SE) of male, female, and juvenile Swan Geese during three different periods of brood rearing in 2002 and 2003 in Heidelberg, Germany. Each family was sampled between one and five times during each period. The mean of each family per period was used to calculate percentages to not over-represent some families. Differences between either males or females and goslings are expressed as * $P < 0.05$; ** $P < 0.01$.

	Feeding	Resting	Walking	Comfort	Vigilant	Agonistic
FAMILIES	Weeks 1–4					
<i>n</i> = 13						
Male	27.7 \pm 3.0 ^{b**}	3.2 \pm 1.6	2.5 \pm 0.8	10.6 \pm 4.0	51.1 \pm 4.1 ^{a**}	4.2 \pm 1.0
Female	41.4 \pm 4.7 ^{b**}	4.8 \pm 2.0	2.2 \pm 0.7	7.0 \pm 2.1	39.9 \pm 4.9 ^{a**}	3.8 \pm 1.1
Juvenile	75.5 \pm 5.0	11.2 \pm 3.9	5.7 \pm 1.8	5.9 \pm 1.9	0.6 \pm 0.2	0.0 \pm 0
Parental	34.6 \pm 3.4	4.0 \pm 1.5	2.4 \pm 0.7	8.8 \pm 2.7	45.5 \pm 3.7	4.0 \pm 0.9
FAMILIES	Weeks 5–8					
<i>n</i> = 8						
Male	35.1 \pm 8.7 ^{b*}	7.6 \pm 3.4	4.4 \pm 1.5	15.4 \pm 4.5	34.5 \pm 5.9 ^{a*}	1.5 \pm 0.7
Female	29.4 \pm 7.3 ^{b*}	9.6 \pm 3.0	4.4 \pm 1.5	23.6 \pm 5.0	29.5 \pm 4.1 ^{a*}	1.7 \pm 0.7
Juvenile	62.8 \pm 12.0	10.1 \pm 3.8	2.6 \pm 1.1	18.8 \pm 8.7	4.1 \pm 0.8	0.0 \pm 0
Parental	32.2 \pm 7.5	8.6 \pm 3.0	4.4 \pm 1.5	19.5 \pm 4.7	32.0 \pm 3.8	1.6 \pm 0.7
FAMILIES	Weeks 9–12					
<i>n</i> = 9						
Male	31.8 \pm 6.9 ^{b**}	14.7 \pm 6.5	3.4 \pm 1.3	17.2 \pm 5.2	29.8 \pm 4.0 ^{a**}	1.5 \pm 0.7
Female	37.4 \pm 5.7 ^{b**}	15.3 \pm 5.7	3.8 \pm 1.4	13.7 \pm 5.0	24.4 \pm 2.6 ^{a**}	3.2 \pm 1.3
Juvenile	57.1 \pm 9.2	23.1 \pm 8.8	3.6 \pm 1.0	12.2 \pm 5.8	2.8 \pm 1.1	0.1 \pm 0.1
Parental	34.6 \pm 5.3	15.0 \pm 6.0	3.6 \pm 1.3	15.4 \pm 4.4	27.1 \pm 2.6	2.3 \pm 0.7
FAMILIES	Weeks 1–12					
<i>n</i> = 30						
Male	30.9 \pm 3.3	7.8 \pm 2.3	3.3 \pm 0.6	13.9 \pm 2.6	40.3 \pm 3.1	2.7 \pm 0.6
Female	37.7 \pm 3.3	9.3 \pm 2.1	3.3 \pm 0.6	13.4 \pm 2.4	32.2 \pm 2.7	3.0 \pm 0.6
Juvenile	66.6 \pm 4.8	14.5 \pm 3.3	4.3 \pm 0.9	11.2 \pm 3.0	2.2 \pm 0.4	0.0 \pm 0.0
Parental	34.0 \pm 2.8	8.5 \pm 2.1	3.3 \pm 0.6	13.6 \pm 2.2	36.4 \pm 2.2	2.8 \pm 0.5
Non-breeders	39.1 \pm 6.1	22.1 \pm 6.8	11.3 \pm 2.2	14.4 \pm 4.1	12.8 \pm 2.3	0.0 \pm 0.0
<i>n</i> = 17						

^a Value higher than goslings. Non-breeders depicted for comparison.

^b Value lower than goslings. Non-breeders depicted for comparison.

Means per period (both years pooled) were 3.9 \pm 0.7 (week 1–4), 3.6 \pm 1.1 (week 5–8), and 3.6 \pm 1.0 (week 9–12).

Time Budgets.—Non-breeding adults spent less time vigilant (Table 1) compared with male (Mann-Whitney *U* test: $Z = -4.584$, $P < 0.001$, $n = 30$), female ($Z = -3.998$, $P < 0.001$, $n = 30$), and parental vigilance (mean of male and female in each pair: $Z = -4.416$, $P < 0.001$, $n = 30$; based on the overall means from weeks 1–12). Within families, females, spent more time feeding (Wilcoxon test $Z = -2.750$, $P = 0.006$, $n = 13$) during weeks 1–4 but not in weeks 5–8 and 9–12 ($P > 0.05$) and, a lower proportion of time vigilant than males during weeks 1–4 ($Z = -2.202$, $P = 0.028$, $n = 13$), but not during periods 2 and 3 (Wilcoxon-test, $P > 0.05$; Table 1).

Goslings fed more than both their parents and their vigilance was lower (Table 1). Dur-

ing brood rearing, males reduced their vigilance between periods 1 and 3 (Wilcoxon test: $Z = -2.201$, $P = 0.028$, $n = 7$), and their agonistic behavior between periods 1 and 2 ($Z = -1.997$, $P = 0.046$, $n = 6$). Other behaviors did not change ($P > 0.05$). Females reduced agonistic behavior between periods 1 and 2 ($Z = -1.892$, $P = 0.05$, $n = 6$) and vigilance between periods 1 and 3 ($Z = -2.197$, $P = 0.028$, $n = 7$).

Parental Care.—Mean parental care (vigilance) per period varied (Table 1). There was correlational evidence for an adjustment of parental vigilance to brood size for periods 1 and 3 (period 1: $r = 0.557$, $P = 0.048$, $n = 13$; period 2: $r = 0.617$, $P = 0.10$, $n = 8$; period 3: $r = 0.753$, $P = 0.019$, $n = 9$). Vigilance was dependent on brood size and period but not year (Total model: $F_{6,23} = 7.847$, $P < 0.001$; brood size $F_1 = 16.599$, $P < 0.001$;

period: $F_2 = 10.051$, $P = 0.001$; year: $F_1 = 2.446$, $P = 0.13$; all interaction terms: $P > 0.10$). Adults of larger broods were more vigilant and vigilance declined through the stages of brood rearing. The total amount of explained variance was high ($R^2 = 0.672$, corrected $R^2 = 0.586$).

DISCUSSION

Time Budgets.—Non-breeders were less vigilant, similar to the findings of others (Lessells 1987, Forslund 1993). Adult geese of different species with broods usually spend between 15 and 45% of their time feeding and 40–45% vigilant to look for predators to protect and warn their goslings (Afton and Paulus 1992). Other studies also found marked differences among adult males, females, and juveniles within broods (Austin 1990, Schmutz and Laing 2002). Females spend more time feeding than males (Lazarus and Inglis 1978, Lessells 1987, Sedinger and Raveling 1990). Males, in turn, spend more time vigilant, similar to the results of the present study. Juveniles fed during a large part of their time similar to other goose species (Afton and Paulus 1992), because juveniles have higher nutritional demands. Afton and Paulus (1992) also present examples for decreasing vigilance during maturation of broods (also Lazarus and Inglis 1978). I also found a decrease in vigilance in Swan Geese. Thus, my study shows that introduced geese have similar behavioral patterns during brood rearing as wild geese.

Parental Care.—Parental vigilance during the brood rearing period was related to brood size and this relationship extended into the post-fledging period. These results support the “shared” parental investment hypothesis. Differences among studies about parental investment and brood size may be caused by brood size as my study covered a wide range of family sizes from 1 to 10 goslings. Age of goslings may have an important role in affecting vigilance behavior (Forslund 1993).

The major conclusion of the study is that introduced Swan Geese have similar parental care and division of labor between gender compared to wild Swan Geese, and to other *Anser* species.

ACKNOWLEDGMENTS

I appreciate the improvements in English usage made by George Farnsworth through the Association

of Field Ornithologists’ program of editorial assistance. Comments from three anonymous referees improved an earlier version of the manuscript.

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